

# Systematics and distribution patterns of Afrotropical Canaries (*Serinus* species group, Aves, Passeriformes, Carduelidae)

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**Abstract:** A brief comparison of results obtained from a morphological and a molecular approach to canary phylogeny is given. Based on the molecular hypothesis, distribution patterns of species under study in both analyses are reevaluated. In molecular trees, nodes of high bootstrap values in stable clusters support monophyletic species groups also found in the morphological dataset. The respective species show mostly allopatric distribution, similar gross habitat demands and are of younger phylogenetic age than species clustered at deep nodes and/or with low bootstrap values. Distribution patterns of these species are either disjunct or sympatric, and gross habitat demands differ.

**Key words:** systematics, distribution patterns, Carduelidae, Afrotropis

## Introduction

Carduelidae is a family of songbirds spread almost worldwide. It comprises about 140 species, of which 32 (Paynter 1968) to 45 taxa (Sibley & Monroe 1990) are placed within the genus *Serinus* Koch, 1816. Distribution of these species is focussed, with 38 members, in the Afrotropis. Two species of the Afrotropical stock also inhabit the Arabian Peninsula, five occur in the Palaearctic and two in the Oriental Regions. In two recent papers, rapid radiation (Arnaiz-Villena et al. 1999) and systematics and distribution patterns (van den Elzen & Khoury 1999) of this species group were analyzed, using two different methods, a molecular (Arnaiz-Villena et al. 1999) and a combined morphological-ethological approach (van den Elzen & Khoury 1999). As the two studies correspond in some of their results and complement each other, both analyses are summarized here, a short comparison is given and, based on the molecular hypothesis of canary phylogeny, distribution patterns of species under study in both analyses are reevaluated

## Phylogenetic analyses

### Results of the morphological approach

In the systematical analysis, 5 ethological and 6 morphological characters found as synapomorphies in 23 extant canary species were polarized from two outgroups *Fringilla coelebs* and *Chloris chloris* and *P. striolata* and *C. thibetana* (see table 1, details in van den Elzen & Khoury 1999). A first-hand cladogram of all 25 species obtained 5 species groups (see also van den Elzen 1985), later given generic rank, mainly following the nomenclature of Wolters (1979): *Serinus* (sensu stricto, 5 species: *alario*, *citrinella*, *canicollis*, *syriacus*, *pusillus* within this study),

Table 1: Behaviour and plumage patterns of *Serinus* species used for cladistic analysis (nomenclature follows Wolters 1979).

Genus	species	01	02	03	04	05	06	07	08	09	10	11
<i>Fringilla</i>	<i>coelebs</i> /juv	?	0	0	0	0	1	0	0	0	1	0
<i>Chloris</i>	<i>chloris</i>	0	0	0	0	0	0	0	0	0	0	0
<i>Alario</i>	<i>alario</i>	0	0	0	0	1	0	2	2	1	1	0
<i>Serinus</i>	<i>citrinella</i>	0	0	0	0	1	1	0	0	1	1	0
<i>Serinus</i>	<i>canicollis</i>	0	0	0	0	1	1	0	0	1	1	0
<i>Serinus</i>	<i>syriacus</i>	0	0	0	0	1	1	0	0	1	1	0
<i>Serinus</i>	<i>pusillus</i>	0	0	0	0	1	1	2	2	1	1	0
<b><i>Serinus</i></b>		<b>0</b>	<b>0</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>1</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>1</b>	<b>0</b>
<i>Crithagra</i>	<i>leucoptera</i>	?	1	1	0	1	0	0	2	3	?	1
<i>Crithagra</i>	<i>striolata</i>	1	1	1	0	1	0	1	1	3	0	1
<i>Crithagra</i>	<i>gularis</i>	1	1	1	0	1	0	0	2	3	1	1
<i>Crithagra</i>	<i>tristriata</i>	1	1	1	0	1	0	2	2	3	1	1
<b><i>Polioptila</i></b>		<b>1</b>	<b>1</b>	<b>1</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>?</b>	<b>2</b>	<b>3</b>	<b>1</b>	<b>1</b>
<i>Dendrospiza</i>	<i>citrinelloides</i>	1	0	1	0	1	0	2	2	2	0	1
<i>Dendrospiza</i>	<i>hyposticta</i>	1	0	1	0	1	0	2	2	2	0	1
<i>Dendrospiza</i>	<i>scotops</i>	1	0	1	0	1	0	2	2	2	0	1
<b><i>Dendrospiza</i></b>		<b>1</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>1</b>	<b>0</b>	<b>2</b>	<b>2</b>	<b>2</b>	<b>0</b>	<b>1</b>
<i>Serinus</i>	<i>flaviventris</i>	1	1	2	0	0	1	1	1	1	0	1
<i>Crithagra</i>	<i>sulphurata</i>	1	1	2	0	0	0	1	1	1	0	1
<i>Crithagra</i>	<i>donaldsoni</i>	1	1	2	0	0	1	1	1	1	0	1
<i>Crithagra</i>	<i>albogularis</i>	1	1	2	0	0	1	1	1	3	0	1
<b><i>Crithagra</i></b>		<b>1</b>	<b>1</b>	<b>2</b>	<b>0</b>	<b>0</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>0</b>	<b>1</b>
<i>Ochrospiza</i>	<i>leucopygia</i>	1	1	3	1	1	0	0	0	0	0	1
<i>Ochrospiza</i>	<i>reichenowi</i>	1	1	3	1	1	1	1	1	3	0	1
<i>Ochrospiza</i>	<i>atrogularis</i>	1	1	3	1	1	1	1	1	3	0	1
<i>Ochrospiza</i>	<i>citripectus</i>	1	1	3	1	1	1	1	1	3	0	1
<i>Ochrospiza</i>	<i>mozambica</i>	1	1	3	1	1	1	1	1	1	0	1
<i>Ochrospiza</i>	<i>dorsostrciata</i>	1	1	3	1	1	1	1	1	1	0	1
<i>Ochrospiza</i>	<i>xanthopygia</i>	1	1	3	1	1	1	0	1	3	0	1
<b><i>Ochrospiza</i></b>		<b>1</b>	<b>1</b>	<b>3</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>?</b>	<b>0</b>	<b>1</b>

## Characters 01-11

01 attraction call of juveniles: 0= identical to begging calls, short, no frequency modulations; 1= frequency modulated, of long duration

02 Head-up posture (aggressive display): 0= wings spread; 1= head-up posture

03 courtship display: 0= lateral displaying, pivoting; 1= fluffed display, 2= head-up posture, 3= heraldic-eagle display

04 nestbuilding: 0= by ♀ only, 1= also by ♂

05 transport of nesting materials: 0= by ♀ only, 1= also by ♂

06 rump coloration: 0= as colour of back; 1= contrasting

07 ear patch: 0= weak; 1= prominent, contrasting; 2= non-existent

08 moustachial stripe: 0= weak; 1= dark and contrasting; 2= non-existent

09 head pattern: 0= uniform, no supercilium; 1= yellow supercilium; 2= s. black and yellow; 3= s. white

10 juvenile plumage: 0= as adult pl.; 1= different to ad. pl.

11 gape coloration of nestlings: 0= red; 1= blue patches on red

0 = plesiomorphic condition, 1(2,3 in transformation series) = apomorphic conditions, ? = no information

*Ochrospiza* (7 species: *leucopygia*, *reichenowi*, *atrogularis*, *citrinipectus*, *mozambica*, *dorsostriata*, *xanthopygia*), *Crithagra* (4 species: *flaviventris*, *sulphurata*, *donaldsoni*, *albogularis*), *Poliospiza* (4 species: *leucoptera*, *striolata*, *gularis*, *tristriata*) and *Dendrospiza* (3 species: *citrinelloides*, *hyposticta*, *scotops*).

As relationships between genera were still unsolved, the dataset was analyzed with the computer programme HENNIG 86. Six trees were found but are not taken into consideration, as they have only poor solutions and low tree stability with a consistency index of 51. Tree stability in computer-based phylogenetic analyses needs a support of 5 characters per node (Mooers et al. 1995), not given in the dataset of van den Elzen & Khoury (1999) as species outnumbered characters by 25 to 11. Lacking additional clear synapomorphies, the number of taxa was reduced by summarizing characters of species groups supported in the first analysis. Thus only 7 taxa represented 5 canary species groups (genera *Serinus*, *Ochrospiza*, *Crithagra*, *Poliospiza* and *Dendrospiza*) plus the two outgroups (table 1, generic names and details in: van den Elzen & Khoury 1999).

Despite the fact that 11 characters had to support 6 nodes, the HENNIG 86 analyses provided one single tree of rather good quality (21 steps, consistency index 80, retention index 80). It places (fig.1) the *Serinus* species next to the outgroups *Fringilla* and *Chloris* at the base of the tree. Thus *Serinus* is the (phylogenetically older) sister taxon of a monophyletic entity comprising four taxa in two sister groups: *Ochrospiza* plus *Crithagra* on the one hand, *Poliospiza* with *Dendrospiza* on the other.

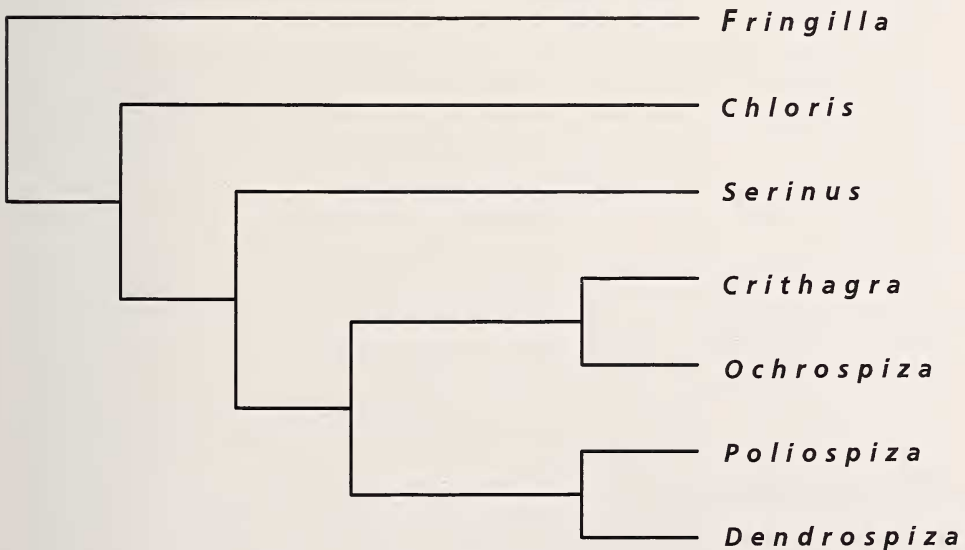


Fig. 1: HENNIG 86-tree from behavioural and morphological characters of species groups mediated under generic names given in table 1.

## Results of the molecular analysis

Arnaiz-Villena et al. (1999) studied 18 (17, if *S. canicollis flavivertex* is treated as a subspecies) “*Serinus*” species using mitochondrial DNA of the cytochrome b gene. Their sample comprises, in the nomenclature put forward in van den Elzen & Khoury (1999), the following species: *Serinus alario*, *S. canaria* (wild birds and domesticated form), *S. serinus*, *S. canicollis* (in two populations *S. c. canicollis* and *S. c. flavivertex*); *Ochrospiza atrogularis*, *O. leucopygia*, *O. citrinipectus*, *O. dorsostriata*, *O. mozambica*; *Crithagra flaviventris*, *C. sulphurata*, *C. albogularis*; *Poliospiza gularis*, *P. striolata*; *Chionomitris thibetana*. As outgroups, DNA sequences of *Fringilla coelebs* and *Passer luteus* were compared, as well as two non-passerine galliform species: *Lophura nycthemera* and *Gallus gallus*. The authors present three dendrograms obtained by three different mathematical procedures (algorithms): unweighted maximum parsimony heuristic search (PAUP), neighbour-joining bootstrap and UPGMA.

In their parsimony and neighbour-joining trees Arnaiz-Villena et al. (1999) show bootstrap values above 50, found in 15 of 20 nodes in the parsimony analysis and 14 of 20 nodes in the neighbour-joining tree. High bootstrap (80 and above) supports nodes and thus phylogenetic relationships of the following species and species-groups in both dendrograms: *Fringilla* as an outgroup to the Carduelidae under study (fig.2: node A); *canaria* and *serinus* (fig.2: cluster D, node 4), *alario* and *canicollis* (fig.2: cluster D, node 3), *flaviventris* and *sulphurata* (fig.2: cluster C, node 2), *atrogularis* and *leucopygia* (fig.2: cluster C, node 1), as sister taxa. Neighbour-joining defended a clade *alario-canicollis-pusillus* (fig.2: D, 3a) and another consisting of *atrogularis-leucopygia-citrinipectus-dorsostriata* (Fig.2: C, 1b). Not shown in fig.2 are the relationships of domesticated and wild *Serinus canaria* (bootstrap 100) and of *Serinus canicollis flavivertex* to nominate *canicollis* (bootstrap 98).

Within all three dendrograms three species-groups were placed concordantly.

– One node (fig.2, D) postulates phylogenetic relationships of species within two subclusters: *canaria-serinus* and *alario-canicollis-pusillus*, and thus supports the morphological-ethological findings and species limits of the restricted genus *Serinus* proposed by van den Elzen & Khoury (1999).

– A second node (fig.2, C, b) places *atrogularis-leucopygia-citrinipectus-dorsostriata* into one cluster that includes not only *mozambica* but also *citrinelloides*, from a different monophyletic unit, the *Dendrospiza*-species group, as depicted in two dendrograms, parsimony and neighbour-joining, but not the UPGMA (see above). A monophyletic relationship of only 5 of these 6 taxa (as members of the genus *Ochrospiza*) was suggested by van den Elzen & Khoury (1999), but the two genera *Ochrospiza* and *Dendrospiza* proved not to be closely related (fig.1). Thus the hypothesis that *Ochrospiza* species are a monophyletic entity is only partly supported.

– A third invariable node (fig.2: C, c) groups four species: *flaviventris*, *sulphurata*, *albogularis*, *gularis*. It also does not support a closer relationship of *Crithagra* species within the limits of the morphological analysis as it places *gularis* into a distinct species group, genus *Poliospiza*. The three tree topologies of the DNA

analysis also do not sustain a broad genus *Crithagra* (sensu Wolters 1979, lumping *Poliospiza* and *Crithagra* species), as they place *P. striolata* either next to *C. thibetana* (fig.2, B, a), and their common node (fig.2, B) in a sister group position to the *Serinus* s.str. node (parsimony tree) or to the node of the Afrotropical clade (neighbour-joining tree, fig.2), or both taxa separately in an outgroup position to the first node of the other 15 species of the whole sample (UPGMA tree).

Of the five lineages proposed by van den Elzen & Khoury (1999), none is unquestionably verified by the mtDNA study. *Serinus* and *Ochrospiza* are partly supported, whereas *Poliospiza* appears to be paraphyletic and the species limits of *Crithagra* may have to be reevaluated. The choice of only one single representative of the *Dendrospiza* species group, *D. citrinelloides*, may have disturbed the tree topology as indicated by the low bootstrap values of 53 and below.

Phylogenetic relationships between the three monophyletic entities described above could not be proved by the molecular analysis. *Serinus* s.str. appears in the three trees figured by Arnaiz-Villena et al. (1999) as the sister taxon to either the Afrotropical clade of van den Elzen & Khoury (1999) (genera *Ochrospiza*, *Crithagra*, *Poliospiza*, *Dendrospiza*; neighbour-joining tree), the *P. striolata*-*C. thibetana* node (parsimony tree), or the *flaviventris-sulphurata-albogularis-gularis* node (UPGMA tree). In the latter, the *canaria-serinus* node is joined by *mozambica* and *citrinelloides* as sister taxa, with the cluster *alario-canicollis-pusillus* in a stable sister-group position.

The parsimony tree depicts a common node of *Serinus* s.str. (including *P. striolata* and *C. thibetana* with bootstrap values below 50) with *Ochrospiza* (including *mozambica*), and with "*Crithagra*" as their sister taxon. The neighbour-joining tree sketches a *Serinus* s.str. cluster opposing a cluster formed by three subgroups, one including the complete sample of *Ochrospiza* species plus *mozambica*, another the "*Crithagra*" subgroup with the already mentioned restriction of *P. striolata*, which forms, combined with *C. thibetana*, the third subset. In the UPGMA dendrogram, *Serinus* species are disrupted by *O. mozambica* and *D. citrinelloides*. Their sister taxon is the mixed *Crithagra*-*Poliospiza gularis* group, and both clusters have *Ochrospiza* species (solely *O. mozambica*) as a sister taxon, opposed by *P. striolata* and *C. thibetana*.

The UPGMA tree in Arnaiz-Villena et al. (1999) also gives an approximate time calculation calibrated on the known divergence time of *Lophura nycthemera* and *Gallus gallus*, 19 Mya. Based on this assumption, *C. thibetana* appears as the phylogenetically most distant and thus oldest species in the sample, diverging about 9 Mya, *Ochrospiza* species are relatively older than the other Afrotropical species under discussion, while the true canaries *Serinus* s.str. are the youngest clade.

### Analyses of distribution patterns

According to the vicariance model of Nelson & Platnick (1981), phylogeny can be inferred from distribution patterns. Speciation is assumed to proceed in geographical isolation, a partial requirement also of the Biological Species Concept (Mayr 1942, 1992). Vicariants are allopatric in their distribution and have similar ecological demands. Therefore species ranges of sister taxa, or of a proposed

monophyletic species group, should be allopatric in early stages of differentiation. It can also be expected that phylogenetically younger species have roughly similar ecological demands and are to be found in more similar habitats than phylogenetically older species but in different niches, as postulated in the extended species concept (Mayr 1992).

Distribution patterns were presented by van den Elzen & Khoury (1999) on counts of species occurrence in 5° x 5° grids. The main sources were the distribution maps in Hall & Moreau (1970), supplemented by individual maps in Ash & Miskell (1998), Clemetn et al. (1993), Gatter (1997), Harrison et al. (1997), Lewis & Pomeroy (1989) and Irwin (1964).

Centres of diversity of Afrotropical "*Serinus*" s.lat. (38 species in Sibley & Monroe 1990) are montane habitats of the Albertine Rift Mountains where 12 species occur. Three minor centres with 8 species each are in the Angolan, east Zimbabwean and Eastern Arc Mountains. West Arica is poorest, with a species maximum of 3 and an average of 1.7 within 5° grids, montane areas in East Africa, with an average of 7.4 species per square, are richest in canary species abundance. Counted by altitudinal distribution, lowland species outnumber montane taxa: 21 versus 15. Two species (*S. canicollis* and *Dendrospiza scotops*) are occurring in both habitats (details in van den Elzen & Khoury 1999).

The four species groups which were separated as the genera *Crithagra*, *Ochrospiza*, *Poliospiza* and *Dendrospiza* from *Serinus* s.lat. are genuine Afrotropical inhabitants. Most species of the genus *Serinus* s.str. breed in restricted ranges around the Mediterranean basin, *Serinus pusillus* occurs from Turkey into the Himalayas, whereas *Serinus canicollis* and *Serinus (Alario) alario* inhabit the Afrotropical region. The two species used as outgroups in the HENNIG 86 analysis, *Fringilla coelebs* and *Chloris chloris*, are distributed in the Palearctic region. *Fringilla* reaches the African continent and has breeding populations in the Canary Islands and parts of North Africa. *Chloris chloris* has its nearest relatives in the Himalayas.

Within the Afrotropical endemic genera, species ranges were found to be allopatric to parapatric in most cases or, if sympatric, species are separated by diverging ecological requirements (details in van den Elzen & Khoury 1999). Centres of species diversity for *Poliospiza* and *Dendrospiza* are montane in the northeastern Rift Valley, for *Crithagra* montane to lowland areas in southern Africa, and for *Ochrospiza* lowlands in northeastern Africa. A topographical divergence of lineages, that is adaptation of species of any of the proposed genera to either montane or lowland habitats, could not be confirmed. As each has representatives in both environments, genera can only be characterized by their distribution centres. As indicated by the ranges of different *Serinus canicollis*-populations – reaching from high altitude montane areas in East Africa to man-made environments in southern Africa – landscape requirements are seemingly not key factors for habitat choice of the species.

As large-scale investigations have shown, distribution patterns are known to correspond best to climatic factors (O'Brien 1998). Van den Elzen & Khoury (1999) explained canary distribution ranges and patterns by climate and climatic changes in the past leading to habitat fluctuations and shifts. The geographic posi-

Table 2: Nodes from the neighbour-joining tree of Armaiz-Villena et al. (1999; fig. 1b) and their interpretation. N.s.= not shown, bootstrap lower than 50; allopatric distribution of species clustered by the node, parap.= parapatric distribution of species, symp.= sympatric distribution; EK coincidence=nodes also confirmed by van den Elzen & Khoury (1999); ntaxa= number of taxa clustered by node; taxa relations= number of taxa per sister group; taxa concerned= taxa clustered belong to different: family= families, genera= to different genera, genus= different species of one genus (limits of van den Elzen & Khoury 1999); n.p.= node not presented in the time calculation tree of A-V. (6+) phylogenetic age judged from different node.

Node	A	B	C	D	a	b	c	1c	1b	1a	2a	3a	1	2	3	4
bootstrap	100	100	n.s.	65	n.s.	n.s.	63	n.s.	80	56	50	89	82	100	96	98
tree stability	no	no	no	yes	partl	no	yes	no	yes	yes	yes	yes	yes	yes	yes	yes
distribution	allop.	symp.	symp.	parap.	allop.	symp.	symp.	allop.	allop.	allop.	symp.	allop.	allop.	parap.	allop.	allop.
habitat	differen t	differen	differen	differen	unknown	similar	differen	differen	similar	similar	differen	similar	similar	similar	sim/diff	similar
EK coincidence	yes	no	no	yes	no	no	no	no	yes	yes	no	yes	yes	yes	yes	yes
ntaxa / taxa relations	18 5/12	12 2/10	10 6/4	5 3/2	2	6 1/5	4 1/3	5 1/4	4 1/3	3 1/2	3 1/2	3 1/2	2	2	2	2
taxa concerned	family	genera	genera	genera	genera	genera	genera	genera	genera	genera	genera	genus	Sspec	Sspec	Sspec	Sspec
phylogenetic age	17 mya	n.p.	n.p.	6 mya	n.p.(9+)	n.p.(6+)	n.p.(6+)	n.p.(6+)	6+mya	5+mya	genera (6+)	5mya	5mya	2+mya	4+mya	4mya

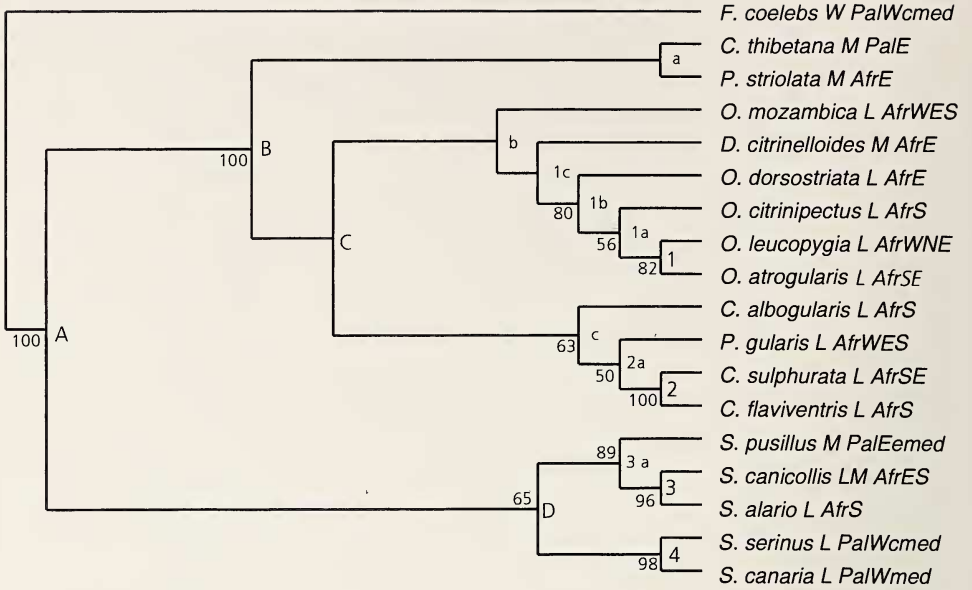


Fig.2: Neighbour-joining bootstrap tree from Arnaiz-Villena et al. (1999, fig.1b), slightly modified. Neighbour-joining (1000 replications) based on 924 bases of mtcyt b genes from 17 canary species and *Fringilla coelebs*. Bootstrap values above 50 are shown. For details see text.

tion of the areas of canary diversity coincides with endemic bird areas already outlined for Africa by Bibby et al. (1992) and Stattersfield et al. (1998) and with areas of primary montane and temperate floristic elements (Miehe & Miehe 1994, Wickens 1976). Ecological requirements in terms of food plant species were not discussed but may count as a limiting factor as most of the canary species are pure seedeaters and thus dependent on food plants, but the requirements of only a few species are as yet documented, including generalists (*Serinus syriacus*, Khoury 1998a,b) as well as specialists (*Polioptila leucoptera*, Milewsky 1976, 1978). Provided with a new hypothesis of "*Serinus*" phylogeny, the neighbour-joining tree of Arnaiz-Villena et al. (1999) was chosen to test topographical and geographical distributions of canary lineages under the vicariance model again. The neighbour-joining tree was favoured because of its convincingly high bootstrap values. Moreover it depicts the phylogeny of genera suggested by the analysis of behavioural and morphological characters carried out by van den Elzen & Khoury (1999). It is presented in fig.2 with slight differences from the original: the two non-passerine species are omitted and nodes for nominate *Serinus c. canicollis* - *S. canicollis flavivertex* and of *Serinus canaria* for wild and domestic forms suppressed.

Under the premises of the vicariance model, nearest neighbours showing up in the dendrogram should verify the following characteristics: allopatric ranges, similarity in their topographic distribution and broad habitat requirements if they are young nodes. Deep nodes in contrast are allowed to display either sympatry, broad habitat differentiation, or lowland-montane divergence, or even show



differentiation in all premises within but not between subclusters. Results of an analysis of the molecular tree are summarized in table 2, and details are also shown in fig.2.

For the first-species pair supported by high bootstrap ancestral nodes, *Serinus canaria-S. serinus*, (fig.2: 4) ranges are allopatric with a small parapatric zone and their ecological requirements are roughly similar, with *S. serinus* having a larger range in more diverse habitat types and at lower elevations. In the *S. alario-canicollis-pusillus* clade (fig.2: node 3a) distribution patterns are puzzling. The allopatry argument is proven, two montane species combined with a lowland form, two Afrotropical canaries combined with a Palearctic species. *Serinus canicollis* and *alario* overlap in distribution in the southernmost parts of their range, where they even associate in mixed-species flocks.

If the distribution patterns of the entire *Serinus* clade (fig.2: node D) are investigated, no range overlap between the species can be found.

The second well-established pair by bootstrap is *Crithagra flaviventris-sulphurata* (fig.2: node 2). Species ranges are allo- to parapatric, overlap occurs in the southernmost part of range, but breeding habitats differ distinctly in the sympatric situation, *C. sulphurata* preferring in general moister habitats at higher altitudes than *C. flaviventris*. The assemblage of *C. sulphurata-flaviventris* plus *P. gularis* (fig.2: node 2a) together with *C. albogularis* (fig.2: node c) sketches a situation not as easily interpreted. *P. gularis* and *C. albogularis* both share the *flaviventris* habitat demands, and the ranges of the congeners *albogularis* and *flaviventris* overlap.

In the third high bootstrap node (*O. leucopygia-O.atrogularis*, fig.2: 1) species with allopatric distribution are again combined: both are savanna inhabitants, *O. leucopygia* living in the drier environment. The taxa adjoined to this species pair in node 1b and 1a by also high bootstrap, *O. citrinipectus* and *dorsostriata*, are allopatric and have roughly equal ecological requirements. If *mozambica* and *D. citrinelloides*, their nodes (fig.2: 1c, b) are of low significance, are joined, the latter, as a montane element, is allopatric to all other taxa and prefers woodland. *O. mozambica* – as the most widespread species – occurs in sympatry with *atrogularis*, *leucopygia* and *citrinipectus* (not with *dorsostriata*!), but is found in moister environments. As this species is allopatric to *dorsostriata*, Hall & Moreau (1970) placed both into one superspecies, the *atrogularis*-group comprising the species *atrogularis* (including *reichenowi* and *xanthopygia*), *leucopygia*, *citrinipectus*, as well as *flavigula* into a second one.

The last node (fig.2: a) supports faintly (since it is only of low significance, its bootstrap values are below 50 and are not given by Arnaiz-Villena et al. 1999) the relationship of *C. thibetana* and *P. striolata*. Both species are disjunct, occurring in high altitudes of different biogeographical regions.

Summarizing, it may be concluded that best results (i.e. high bootstrap values, tree stability, concordance with the vicariance model and systematics deduced from the morphological approach) are in the younger nodes, with the exception of node A. The suggested phylogenetic relationships of species in clusters with nodes of low bootstrap values, with inconsistent arrangements according to the algorithms used, are in most cases also contradicted by inconsistent distribution patterns and

broad habitat requirements of the species concerned. Deep nodes (B, C and partly a) are seemingly more difficult to prove than younger ones (from 6 Mya on).

Following the HENNIG 86 tree-topology of genera (van den Elzen & Khoury 1999), *Serinus* s.str. had to be the phylogenetically older clade. The ancestor of this taxon entered Africa south of the Sahara, where radiation of *Ochrospiza*, *Polioospiza*, *Dendrospiza* and *Crithagra* was favoured by mainly Pleistocene climatic changes, whereas *Serinus* s.str.-species (e.g. *Serinus canicollis*) entered the Afrotropics in a second immigration wave (see also van den Elzen 1985).

From their calculations of the phylogenetic age of different canary "lineages", Arnaiz-Villena et al. (1999) concluded that the "*Serinus*"-lineage s.lat. appeared in the Miocene and that Pleistocene glaciations may have driven subspeciation only, the majority of genera in the nomenclature of van den Elzen & Khoury (1999) being already present in their ancestral forms 6-7 Mya. These authors discuss an Asian origin for "*Serinus*", an old hypothesis favoured by Mayr (1946) and Marten & Johnson (1986) for other Carduelidae. Research on this topic will have to continue.

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